In: Progress in Mathematical Biology Research
Editor: James T. Kelly, pp. 191-218.
ISBN 978-1-60456-171-5

Chapter 5

CROSSING THE BORDERS OF SPATIAL ANALYSIS AND MODELLING: A RETHINK

C. Hui*

Centre of Excellence for Invasion Biology,
Department of Conservation Ecology and Entomology,
University of Stellenbosch, Private Bag X1,
Matieland 7602, South Africa

ABSTRACT

Understanding the mechanisms behind the spatial patterns of species distributions is one of the major focuses in theoretical ecology. Spatial modelling techniques such as lattice models and cellular automata bring numerous spatial patterns in ecology. Taking spatial factors into account also helps to solve many puzzles in ecology, such as the paradoxes of diversity, polymorphism and altruism. To analyze the numerous spatial patterns, ecologists introduced the moment approximation from statistical physics. Spatial analysis of species distributions can also finds its roots in the sampling statistics of ecology. Based on aggregation indicators (e.g. Lloyd's indices and joint-count statistics), ecologists are able to distinguish the degree of non-randomness from spatially implicit and explicit perspectives, with over-dispersal and spatial autocorrelation as the synonyms of aggregation, respectively. Such sampling statistics also leads to the occupancy-abundance relationship with valuable applications in conservation. Although both spatial modelling and spatial analysis aim to achieve a profound understanding of species spatial patterns, they barely intersect. Through building the connections between sampling statistics and moment (pair) approximation, we unveil the relationship between the sampling density (mean abundance) and the colonization-extinction process. The intersection also solves the scaling pattern of species distribution by applying the pair approximation and the Bayesian rule into the joint-count statistics. By a scaling metapopulation model, we found that randomness is the bridge linking sampling statistics and spatial modelling, as well as the spatially implicit and explicit patterns. This

* Email: chui@sun.ac.za

intersection also sheds light on the occupancy-abundance relationship and the connection between spatial patterns and species life-history traits. In this exercise, we emphasize the importance and potential of bringing these two schools of knowledge together in understanding ecological complexity. Ten merging questions that require this intersection have been presented to expound on possible applications to the species distribution and the community structure in the near future.

INTRODUCTION

Ecology is the study of relationships between organisms and the environment. This classic definition illustrates that the focus of this science is the relationships (or interactions) between individuals, populations, species, and even communities. Shaped by the golden age of theoretical ecology (1920-1940), ecologists mainly deal with the abundance and distributions of populations in time and in space, i.e. the spatiotemporal dynamics. Why can this species survive here? How many individuals (or species) are out there? These questions have been largely explored by mathematical models and experimental tests. Early studies of the dynamics of biological populations tended to look for a stable equilibrium in spatially homogeneous contexts (Pielou, 1969; Murray, 1989). For a single species, density-dependent mechanisms, such as the Allee effect and the overcrowding effect (self-thinning), control the population level within the environmental carrying capacity. For multiple species, interactions such as competition, predation, parasitism, epidemic transmission, facilitation, and cooperation have been clarified as to their effect on community structure and dynamics. In particular, ecological relationships, such as competition, predator-prey and host-parasite, have been deeply analyzed by mathematical models, such as the Lotka-Volterra equations. At one stage, ecologists believed that all the equilibriums of ecological systems had been (or would soon be) found and therefore all the questions would be answered, but two events frustrated that hope.

First, May (1974) found that a simple discrete logistic model could generate a chaotic dynamics. With the increase of the intrinsic growth rate, the equilibrium of the system jumps from a stable attractor to an oscillator, and finally to a chaotic attractor. This complicated behavior of the dynamics is different from those caused by environmental noise, and therefore was given the name deterministic chaos. Hui and Li (2003) suggested that over the past 30 years, a vastly complicated picture has emerged for the range of temporal behaviors that populations can exhibit. This is mainly due to the nonlinearities of biological production function (Roughgarden, 1997). A primary mechanism generating the complex dynamics is the density-dependent factor in population growth equations, such as the logistic function. Methods like ordinary differential equations, phase plane and bifurcation diagrams in the dynamic analysis have become the principal approaches in studies of temporal dynamics (Begon et al., 1996).

Second, the expansion of ecological research interests from simple interactions, to large- or macro- systems has caused prosperity in community and ecosystem studies. The theoretical and empirical research on spatial interactions has accumulated recently, resulting in the prosperity of spatial ecology (Tilman and Kareiva, 1997) and landscape ecology (Pickett and Cadenasso, 1995). “Spatial” and “scaling” have become two dominant words in recent works. Levin (1992) further suggested that ecology is in fact pattern recognition at different scales.

In the mean time, spatial ecology has been coined the "final frontier" of ecology (Liebhold et al., 1993). The most important discovery of spatial dynamics is the self-organized distribution pattern, even in homogeneous patchy environments (Hassell et al., 1991, 1994; May, 1994). Like the self-structured limit cycles in temporal dynamics, self-organized spatial patterns come from interspecific interactions as well (e.g. Hui, 2004; Hui et al., 2004). Among different modeling frameworks that include spatial structure, there are three broad categories (Hastings, 1994). One framework is based on reaction-diffusion models (Levin, 1974), which can be either discrete or continuous in time and space. A second framework is based on looking at metapopulations by considering the number of patches in different states (Levins, 1969; Hanski, 1991a, b, 1999; Hui and McGeoch, 2006, 2007a; Hui et al., 2006). A final framework is based on cellular automata and contact processes (Czaran and Bartha, 1992; Durrett and Levin, 1994; Walters, 2001; Hui et al., 2004, 2005). These two findings (i.e. chaotic and spatial factors in ecological research) bring forth the flourish of new concepts in ecology: pattern formation and recognition. The idea of a self-organized complex adaptive system becomes a new understanding of the evolutionary, ecological, biological system.

The classic paradox (e.g. the paradox of diversity) (Hutchinson, 1961) left in the golden age has been elegantly solved (e.g. colonization-competition trade-offs) (e.g. Horn and MacAruthur, 1972; Levin and Paine, 1974; Platt and Weis, 1977; Tilman, 1994). New models for understanding the persistence of species have been developed (such as the metapopulation model) (Hanski, 1999). Methods from physics have been brought in to solve the complexity in ecological dynamics (such as 1/f-noise and spectrum analysis) (Gisiger, 2001). Landscape ecology and macroecology have flourished due to the progress of computer hardware and programming (Pickett and Cadenasso, 1995) and the accumulation of large-scale data (Gaston and Blackburn, 2000). Virtual and digital ecology have been founded and begun to move this real world into cyberspace. It's time for us to synthesis all these spatial patterns so that we can see where the future of ecology lies.

LATTICE MODELS

To understand the self-organized pattern in spatial ecology, cellular automata and lattice models have become a common framework to generate and explore spatial patterns. These kinds of models were originally invented by Stanislaw Ulam and John von Neumann at the Los Alamos National Laboratory to simulate the growth of crystals and self-replicating systems. In the 1970s, John Conway used the cellular automaton in his "game of life". These methods were brought into theoretical ecology and biology from the 70s to 90s (Maynard Smith, 1974; Wolfram, 1984; Rand and Wilson, 1995). Cellular automata and lattice models not only present numerous spatial patterns that are generated by local ecological interactions, but also show insights into solving puzzles in traditional ecology. Here, I list three examples of how lattice models assist in introducing spatial factors into ecological perspectives and subsequently solve various dilemmas in ecology.

The first example is concerns the paradox of biodiversity (Hutchinson, 1961). According to the competitive exclusion principle (Gause, 1935; Huffaker, 1958), there is no identical species (in terms of their niche) that can coexist at the same place. However this theoretical truth was challenged by a real example from nature. Hutchinson (1961) noted that a well-

mixed pond with few limiting nutrients contains more than a hundred species of phytoplanktonic algae. Competing superiors can not simply exile the weaker. Although according to Tilman's resource competition model (Tilman, 1977, 1982), potentially unlimited species can coexist on a single limited resource provided that those species are separated on nutrient gradients, however the relatively narrow range of resource gradient in a pond eliminates the possibility of a large number of algae species coexisting. This paradox of diversity also exists in plant communities. For example, the Succulent Karoo biome in southern Africa is one of the twenty-five hotspots of biodiversity in the world (Myers et al., 2000); nevertheless as a semi-desert region, the soil nutrient gradient is surly not capable of supporting the co-existence of almost 5,000 plant species. Interestingly, in Huffaker's (1958) original study, he also found that persistence was impossible in a small homogenous habitat but was prolonged in larger habitats, which potentially have higher environmental heterogeneity. Using the Levins model, Tilman (1994) showed that any number of species can stably coexist in a spatial homogenous environment, even though the best competitor immediately displaces all others locally (also see Lehman and Tilman, 1997). This spatial coexistence relies on a trade-off between a species' competitive ability and its colonization (dispersal and establishing) ability. Using lattice models, Vance (1984) and Pacala (1986) showed that local competition and colonization cause populations to become aggregated in space. As we can see, adding the spatial factor was the key to solving this paradox. Lattice models revealed the aggregated pattern of each species in space, which fitted the field observations.

The second puzzle in ecology that has been solved from spatial perspectives concerns the evolution of cooperation. Darwin's natural selection is based on individual selection; however, altruistic behavior obviously means cost to its actor. In searching for the approach through which altruistic behavior emerges and persists, scientists have generally presented three theories: group selection (Williams, 1966; Wilson and Sober 1994), kin selection (Hamilton, 1964) and reciprocal altruism (Trivers, 1971; Axelrod and Hamilton, 1981). The theory of reciprocal altruism is based on prisoner's dilemma games (PDG) (Harms, 1999; Hoffmann 2000; Nowak and Sigmund, 2004; Hui et al., 2005; Zhang et al., 2005a; Hui and McGeoch, 2007b). To defect is the evolutionary stable strategy and the Nash equilibrium in the PDG (Axelrod and Hamilton, 1981), the successful invasion of the cooperators into defectors, is almost impossible; even the resistance of cooperators to defector's invasion becomes difficult. This incurs the paradox of cooperation. The efforts to break this deadlock lead to the construction of complex strategies based on the iterated PDG, such as the famous Tit-for-Tat (Axelrod, 1984) and Win-stagy Lose-go strategies (Nowak and Sigmund, 1993). Spatial models have also been introduced into the PDG to resolve the paradox (Nowak and May, 1992). These spatial PDG were focusing on the dynamics of the relative frequency of each behavioral strategy within a constant population (Nowak et al., 1994; Nowak and Sigmund, 2004). Hui et al. (2005) and Zhang et al. (2005a) studied the effect of spatial PDG on the population size as well as the effect of habitat destruction on the relative frequency of behavior strategies within the population. A stage-equilibrium hypothesis (that species adjust the frequency of its behavior strategies and maintain its population size) was presented to capture the system behavior when facing environmental stress (Hui e al., 2005). Hui and McGeoch (2007b) studied the spatial patterns of spatial PDG's using lattice model and spatial correlation techniques (Hui et al., 2006). Two general results are: (1) the clusters of cooperators in the spatial habitat reduce the interface between cooperators and defectors,

which protect the cooperators; (2) the metapopulation of mixed strategies could even flourish when facing mild to moderate stress (e.g. habitat destruction) due to the overcompensation of cooperation rewards for extinction debt (Hui et al., 2005).

The third example is the solution of Fisher's (1930) paradox (polymorphism vs. genetic load) (Hanski and Zhang, 1993; Hui and Yue, 2005). In 1930, Fisher proposed the famous "fundamental theorem of natural selection", indicating that fitness can be maximized in a pure-line population (Fisher, 1930). This theorem has received much criticism because it does not accord with the numerical experimental results which demonstrate that polymorphism is popular in nature (Wright, 1930; Haldane, 1930). Since then, debates between selectionists and neutralists have never reached a resolution about the high polymorphism in natural populations (Kojima and Yarbrough, 1967; Kimura, 1983). Although natural selection acts on different individuals within a species, the pathway of biological evolution rarely resorts to intraspecific competition. Phenotypic plasticity is a universal phenomenon for species to face environmental changes and heterogeneity (Miner et al., 2005), for example, induced mutation is a prevalent mechanism in insects which reduces the intensity of intraspecific competition (Clark et al., 1967). This may be ascribed to the fact that intraspecific competition between different genotypes incurs a high genetic load for the species. Maintaining polymorphism by selection may itself entail an enormous and intolerable genetic load (Strickberger, 2000). In fact, a balanced polymorphism might be pursued through heterozygote superiority, or overdominance (Ford, 1940; Dobzhansky, 1970), yet it also incurs a high genetic load. Inspired by Levins' original idea that both the spatial and temporal organization of the environment might significantly affect the extent to which a population would rely on genetic polymorphism (Levins, 1968), Hui and Yue (2005) found that using lattice models, the feedback between organism and environment generate archipelago-like structures in space through an ecological imprint in order to maintain polymorphism with low genetic load within demes, which does not require heterozygote superiority. This ecological inheritance caused by niche construction (Odling-Smee et al., 1996) could be the major mechanism of fine-scale heterogeneity in species habitat (Hui et al., 2004; Han et al., 2006). Hence, Fisher's puzzle can also be solved by taking space into account. Cellular automata and lattice models are the powerful tools that bring spatial factors into the reality of spatial patterns.

Not only can cellular automata and lattice models solve those dilemmas and paradoxes in traditional ecology (due to small scale and lacking of spatial or heterogeneity factors), they also serves as an important method to find new insights in ecology. For example, the Allee effect, caused by the social dysfunction and failure to mate successfully when population density falls below a certain threshold, is one of the most important phenomena in population ecology (Allee, 1931, 1938; Asmussen, 1979; Viet and Lewis, 1996; McCarthy, 1997; Grevstad, 1999; Berec et al., 2001). Normally, ecologists only care about the threshold (or founder) phenomenon caused by the Allee effect when the population size is small (McCarthy, 1997; Wang et al., 1999); but when bringing spatial factors into account, the Allee effect becomes a strong factor in influencing species dispersal and distribution range (Viet and Lewis, 1996; Metz et al., 2000; Keitt et al., 2001). Hui and Li (2004) developed a continuous dynamic model by pair approximation and two-dimensional spatial lattice models to describe the influences of Allee effects on the distribution and dynamics of metapopulations. They found that the original global stable equilibrium of metapopulation size turns into a local stable equilibrium with Allee effects, which is sensitive to the initial situations that can incur a threshold phenomenon in dynamics. When the intensity of the

Allee effect varies within a certain range, a new positive local stable equilibrium appears (Hui and Li, 2004). Simulation results from the lattice models reinforce that the new equilibrium forms a static distribution border in space, which could be a new explanation for the species' current distributional range.

Moreover, lattice models suit the quadrat sample design in experimental ecology and therefore have been widely adopted in ecology for species surveys. Dividing space into quadrats in sampling is a simple but powerful method to estimate species abundance, spatial distribution and community structure (Figure 1). Lattice data are normally obtained from two kinds of experiments. One is from controlled laboratory experiment, in which patches are designed in a two-dimensional lattice way. For example, to explore the spatial structure of the fruit fly (Drosophilidae) community, Warren et al. (2003) arranged a 12×18 decaying nectarine fruit matrix (also see Hui et al., 2006). The other one is by dividing continuous space into lattices. For example, the bird atlas of southern Africa employed this typical lattice sample deign with each lattice representing a quarter-degree quadrat (Harrison et al., 1997). He and Gaston (2000) and Hui and McGeoch (2007) divided real plant distribution into presence-absence map to explore the occupancy-abundance relationship. Kunin (1998) used the artificial divided lattice networks addressing the scaling issues of species distributions in the United Kingdom (also see Hartley and Kunin, 2003; Wilson et al., 2004). Harte et al. (2005) and He and Legendre (2002) analyzed the relative abundance patterns and species-area relationships in communities by using lattice networks. Hui and McGeoch (2007) explored the occupancy frequency distribution in communities by using a lattice as a means of division. This all indicates that lattice models are not only dominant in theoretical studies but also in experimental ecology. Spatial analysis will normally deal with the data generated from lattice models or designs. Isolated studies from either side (theoretically or experimentally) block communication in ecology. Their potential link will be unveiled in the following sections.

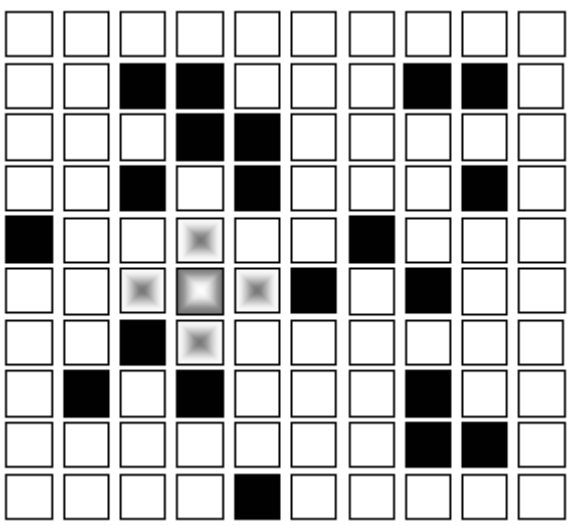


Figure 1. A schematic illustration of a presence (■) - absence (□) map. The four gray rectangles demonstrate the four von Neumann neighbors of the centre one.

SPATIAL ANALYSIS

Understanding the patterns of species distribution, such as aggregation and randomness, is one of the central problems in ecology (Gaston and Blackburn, 2000). It is a problem not only of intrinsic interest, but of essential importance in the final resolution of patterns in macroecology (McGeoch and Gaston, 2002). Current ecological research aims, not only to analyze the patterns generated by various conditions in a two-dimensional map, but also to understand the mechanism underlying those patterns to the extent that predictions can be made. As mentioned above, distribution patterns of species have been well studied by mechanistic approaches (by theoretical ecologists), such as metapopulation dynamics that reveal the ecological processes leading to present distributions (Hanski and Gilpin, 1997; Tilman and Kareiva, 1997; Dieckmann et al., 2000; Hui and Li, 2004; Zhang et al., 2005b), and statistical analysis (by experimental statisticians), such as spatial autocorrelation indices that focus on the patterns of species distribution *per se* in an attempt to seek suitable methods of description (Li and Reynolds, 1995; Dungan et al., 2002; Fortin et al., 2002; Perry et al., 2002). These two approaches are complementary but have scarcely been combined. This lack of collaboration was because the former deals mainly with spatial patterns from computer simulations and mathematical models, whereas the data that the latter deals with comes from real experiments and surveys. Their research objects also differ. Theoretical studies concentrate on revealing the mechanisms behind (why and how); whereas the experimental studies care about comparison (what, how much and how many). It is healthy to link them together by their similar essence and further bring new insights into spatial ecology.

In the spatial analysis of the real experimental and landscape data, a presence-absence map (a binary spatial data) is the easiest and quickest representation, which can be provided for a large-scale region with relatively little costs (e.g. Fielding and Bell, 1997). The spatial niche modelling (such as the climatic envelope; Kadmon et al., 2003) can also provide a quick, large-scale presence-absence map for focal species' distribution range. Climatic envelope modelling also provides a quick way to trace the effect of climatic changes. As mentioned above, lattice models and samples also provide a huge amount of binary data from theoretical and experimental studies. Two issues were shown up in the analysis of presence-absence data: one is the spatial pattern of the distribution; the other is the scaling sensitivity of the range (formally called mapping unit viable problems MUVP; e.g. Wu et al., 2006). The former includes the size of the distribution (range size), spatial structure of the individuals; the latter studies how the result of spatial analysis responds to the size (grain and extent) and effort of samples. Besides these two spatial and scaling issues, understanding the potential mechanisms triggering particular spatial patterns was also one of the major research interests.

SPATIALLY IMPLICIT PATTERNS

To categorize the spatial patterns obtained, we have to clarify some definitions in spatial analysis. Statistical ecologists normally distinguish species' distribution patterns into aggregation, randomness and others (such as uniformity and segregation), without clarifying whether these categories are spatially implicit or explicit. This confusion brings lots of problems in the comparison of each other's works and hinders the further meta-analysis in

this field. Due to the different observations and ecological consequences of using spatially implicit and explicit approaches (Veldtman and McGeoch 2004), a distinction must be made between distribution patterns in a statistical (spatially implicit) sense and those in a spatial (explicit) sense (Dungan et al., 2002; Perry et al., 2002). These categories of spatial patterns are closely related to the definition of heterogeneity (Li and Reynolds, 1995; Wiens, 2000; Dungan et al., 2002). Here, I simply distinguish the distribution patterns of species into spatially implicit and explicit. I use the term spatially implicit when describing the statistical heterogeneity in samples without regarding the relative locations of these samples. The term spatially explicit will be used when the relative locations or spatial information of samples were concerned.

OVER-DISPERSAL

From the point of view of experimental ecologists, the key question is to describe the (spatial) patterns and compare them with those from different species, or from different places, or time, etc. Traditionally, ecologists described the spatial pattern without spatial input, for example, an "aggregated" population means the number of individuals in samples are over-dispersed (the variance-mean ratio σ_a^2 / μ_a is greater than one, where a is the grain size). Using the variance-mean ratio to judge the aggregation ($\sigma_a^2 > u_a$), randomness ($\sigma_a^2 = u_a$) and uniform ($\sigma_a^2 < u_a$) of species distributions coincides with that using coefficient of diffusion (also called index of dispersion; Pearson and Hartley, 1966; Elliott, 1977) to discern distribution patterns.

The relationship between the variance and the mean of abundance can be described by Taylor's power law, $\sigma_a^2 = c \cdot u_a^b$, where c and b are constants (Taylor, 1961). Although there is still a controversy around the mechanism and meaning of Taylor's power law (see a review by Kendal, 2004), this robust rule has been tested for more than 400 species (Taylor et al., 1978; Taylor and Woiwod, 1982) and also manifests with other seemingly disparate processes (Anderson and May, 1988). Another robust rule is the linear relationship between grain a and mean abundance observed from samples $u_a = a \cdot d$, where d is population density (Hubbell, 2001). This relationship was simply because the mean abundance μ_a equals the total number of individuals in the sample extent *N* divided by the number of grains in the extent, *A/a*. Therefore, the coefficient of diffusion will be,

$$\frac{\sigma_a^2}{u_a} = c \cdot d^{b-1} \cdot a^{b-1} \tag{1}$$

As Downing (1986) observed, the vast majority of estimates for b range between 1 and 2. Only 2% of observations were above 2, and about 0.6% below 1 (Downing, 1986; Kendal, 2004). In equation (1), if parameter b is below 1, the coefficient of diffusion (1) will lead to infinity with the decrease of grain a, which is biologically unrealistic. Consequently, the

assumption that exponent b is above 1 would not only have a theoretical explanation (Keeling and Grenfell, 1999) but also be supported by rich data (Downing, 1986). Under this assumption, the variance-mean ratio in equation (1) will change from zero to infinity as scaling up occurs (the increasing of grain a); thus, the statistical distribution patterns of species will change from uniformity to randomness, and finally to aggregation. It implies that the variance will increase more rapidly than the mean abundance with spatial scale and the statistical heterogeneity will increase with grain.

Another way to understanding the over-dispersed pattern is to have a look at the abundance frequency distribution in samples. Let p_n be the fraction of samples with n individuals. For an over-dispersed (aggregated) population, a negative binomial distribution was found to fit this sample result well,

$$p_n = \binom{k+n-1}{n}\left(\frac{\mu}{\mu+k}\right)^n\left(\frac{k}{k+\mu}\right)^k \tag{2}$$

where μ is the mean abundance as above and *1/k* is a parameter describing the degree of aggregation (note that in fact 1+*1/k* is the Lloyd's index of crowding; Lloyd 1967). When k is less than one, we expect an aggregated population. When k limits to infinite, the negative binomial distribution becomes a Poisson distribution, describing a random distribution. He and Gaston (2003) revised this distribution by replacing *k* with $\mu^2/(\sigma^2-\mu)$, inspired by Taylor's power law (Taylor 1961). Wiens (2000) suggested calling these kinds of indices the "non-spatial" ones, such as *k*, the variance-mean ratio, Lloyd's I_L and Morisita I_M (e.g. Hulbert, 1990). Some of these indices have also been criticized by Hulbert (1990) for their inconsistency in distinguishing the distributions of "Unicorns".

The interesting thing when considering the abundance frequency distribution in samples is not about the non-spatial index *k*, but the occupancy-abundance relationship. For simplicity if we only care about the occurrence of samples with more than one individual ($n \geq 1$), p_+, we have an occupancy (p_+)-abundance (μ) relationship. For the improved negative binomial distribution (He and Gaston, 2003), the occupancy-abundance relationship will be,

$$p_+ = 1-\left(\frac{\mu^{1-b}}{c}\right)^{\frac{\mu^2}{c\cdot\mu^b-\mu}} \tag{3}$$

Of course, there are different forms of occupancy-abundance relationship from different perspectives. For example, if individuals were randomly distributed, the occupancy-abundance relationship will simply be $p_+ = 1-Exp(-d)$. The negative binomial distribution has a occupancy-frequency distribution as $p_+ = 1-(1+\mu/k)^{-k}$. Hui and McGeoch (2007c) reviewed all these occupancy-abundance relationships and summarized them as a percolation process. A "droopy tail" model has been invented to catch the characteristics of the occupancy-abundance relationship. Although occupancy, or range size,

can only capture the size of a spatial distribution, it has its special importance in conservation as it provides a quick and efficient way to predict abundance from occupancy (He and Gaston, 2000; Holt et al., 2002; Hui and McGeoch, 2007c).

LEVINS MODEL

The negative binomial distribution as well as the other indices above tells us what the species distribution looks like from a statistical (non-spatial) perspective. Nonetheless, we still don't have a clue how the species ends with such a pattern. From the theoretical ecologists' perspective, this problem can be solved. Using a metapopulation framework (Hanski, 1999), a species distribution in space or a suitable patch networks is due to a balance of colonization and local extinction (within patches). The term 'metapopulation' describes a 'population' consisting of many local populations. All local populations have a substantial probability of extinction, and hence the long-term persistence of the species can only occur at the regional or metapopulation level (Hanski, 1998). The classic metapopulation framework is based on the patch occupant model (Levins, 1969), a simple logistic-like model. The patch occupant model grasps the spatial dynamics of the occupied patches using a contact process. If we don't consider the spatial issues, i.e. assuming colonization is spatial independent, or a well mixed population, or considering a highly mobile population, we have the following occupancy model.

$$\frac{dp_+}{dt} = w \cdot p_+(1 - p_+) - m \cdot p_+, \tag{4}$$

where p_+ is the fraction of patches occupied by the species, w and m are the parameters of the colonization rate and the extinction rate, respectively. As long as $m < w$, the nontrivial equilibrium is globally stable (Hui and Li, 2003; Hui, 2007a),

$$\hat{p}_+ = 1 - \frac{m}{w} \tag{5}$$

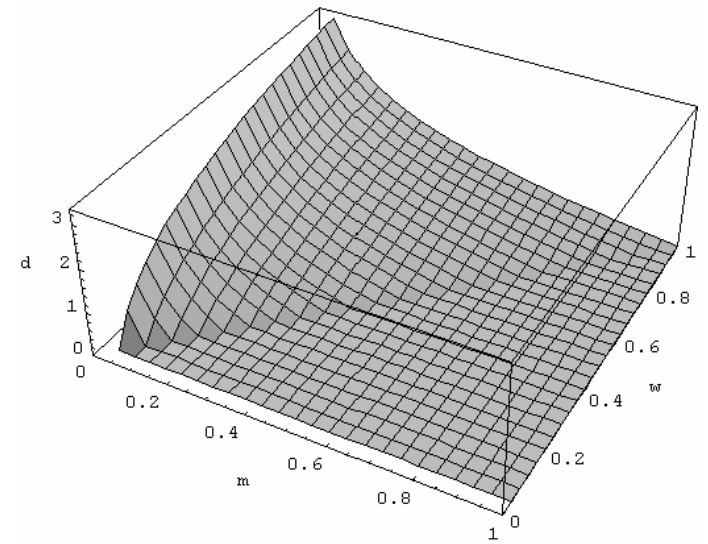
For simplicity, if we only compare equation (5) with the occupancy-abundance relationship from the Poisson distribution, we have (Figure 2a),

$$Exp(-d) = \frac{m}{w}. \tag{6}$$

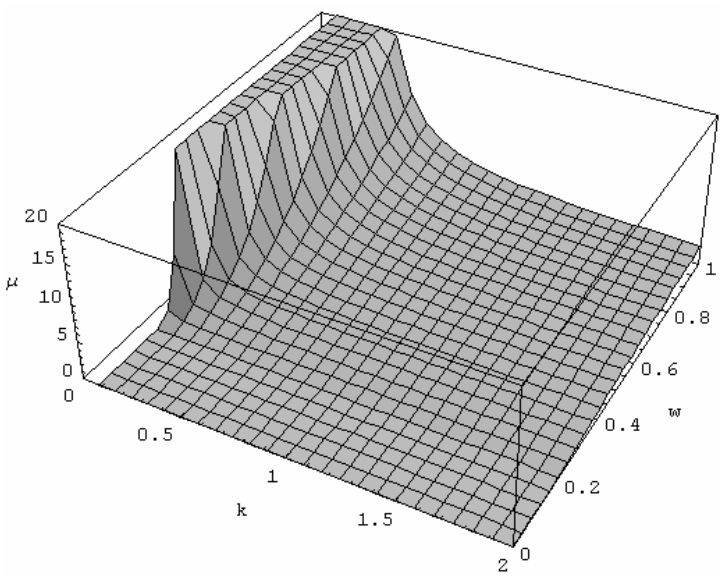
For the occupancy-abundance relationship of a negative binomial distribution, we have (Figure 2b),

$$\mu = k\left(\left(\frac{m}{w}\right)^{-1/k} - 1\right) \tag{7}$$

We found that, firstly, through the link between the two perspectives, we build a relationship between species abundance (population size) with its life-history characters (colonization rate, mortality).



A



B

Figure 2. (A) The relationship between colonization rate, extinction rate, and density of a random distribution; (B) the relationship between aggregation, colonization rate and mean abundance of a aggregated population (m=0.2).

For random distributions (Figure 2A), colonization rate and extinction rate have almost a linear impact on species density. The density can only change within a small range (0~3), which excludes the possibility of a highly abundant species having a Poisson distribution. If we allow individuals to become clustered locally, i.e. a negative binomial distribution (Figure 2B), the upper range of mean abundance increases dramatically with colonization rate especially when *k* is small indicating a highly aggregated species. Note that we only use the simplest version of spatial modelling (Levins model), more advanced models will definitely bring up new findings. This first attempt indicates that there is a huge research space out there when we cross the borders of the fields, spatial analysis and modelling in ecology.

SPATIALLY EXPLICIT PATTERNS

To describe the spatial characteristics of a species distribution, ecologists have invented spatial autocorrelation for describing the missing part of non-spatial patterns. Simply speaking, spatial autocorrelation tells us how many individuals are close to each other (Fortin et al., 2002). Using the same principle, you can also find out the spatial closeness of two different species, normally called species association. Within multiple species (e.g. a community), the same frame work leads to the definition of nestedness. Theoretical ecologists also have to summarize the spatial pattern obtained from lattice models. A method called moment approximation has been introduced into the spatial pattern analysis (Sato and Iwasa, 2000). Analogous to Taylor's series expanding in mathematics, all the spatial patterns can be expressed by a moment approximation. Practically, if we only consider the first- and second-order expression and ignore the higher order, we can have a pair approximation of spatial pattern. Moment approximation of spatial pattern and spatial autocorrelation have similar frameworks when analyzing spatial patterns. However, the comparison between these two methods has hardly been touched in ecology. Here I demonstrate their inner relationships by comparing some typical methods in each framework.

JOINT COUNT STATISTICS

In the spatial analysis from experimental and landscape ecologists, there are a group of indices dealing with the distance sensitivity of spatial patterns, called LISA (local indicators of spatial association) (Anselin, 1995). The simplest index from LISA to describe the spatial pattern is the joint-count statistics (Fortin et al., 2002). Joint-count statistics is the first step to describe real spatial patterns by giving the status of its neighbors (adjacent patches). If we only care about two status, presence and absence (Figure 1), instead of the exact number of individuals in it, we have four states with regard to the focal patch and its randomly-chosen neighbor: an occupied cell with a neighbor that was also occupied, $q_{+/+}$; an occupied cell with an empty neighboring patch, $q_{0/+}$; an empty cell with an occupied neighbor, $q_{+/0}$; an empty cell with an empty neighbor, $q_{0/0}$. In fact we only need two variables (p_+, $q_{+/+}$) to express all the other joint-count statistics:

$$
\begin{aligned}
p_0 &= 1 - p_+ \\
q_{0/+} &= 1 - q_{+/+} \\
q_{+/0} &= (1 - q_{+/+}) p_+ /(1 - p_+) \\
q_{0/0} &= (1 + q_{+/+} p_+) /(1 - p_+)
\end{aligned} \tag{8}
$$

There is still an inequality controlling the balance between p_+ and $q_{+/+}$, $0 \le p_+ \le 1$ and $2 - 1/p_+ \le q_{+/+} \le 1$ (Hui and Li, 2004). This is the joint-count statistics: simple and elegant. If $q_{+/+} > p_+$, we have a spatially autocorrelated population (or called aggregated). If $q_{+/+} = p_+$, we have a spatially random one. The ratio $q_{+/+} / p_+$ or the difference $q_{+/+} - p_+$ gives the degree of spatial clustering (Fortin et al., 2002; Hui et al., 2006). Of course, the group of LISA can analyze the spatial patterns from not just the presence-absence data, and as a consequence it can provide more information on spatial autocorrelation, i.e. it can describe the clustering of abundance in samples by for example Moran's *I* index (1950). I chose the joint-count statistics here just to demonstrate what and how we can link with theoretical studies in the future.

PAIR APPROXIMATION

Joint-count statistics doesn't tell us the mechanism behind this spatial pattern, i.e. what causes this particular aggregated spatial distribution, yet this question can be solved by describing the presence-absence dynamics. The distribution pattern of species can not only be described by joint-count statistics (Upton and Fingleton, 1985; Fortin et al., 2002), but also by pair approximation, which has similar conceptual and mathematical meanings in spatial and metapopulation ecology (Hanski and Gilpin, 1997; Tilman and Kareiva, 1997; Dieckmann et al., 2000; Hui and Li, 2004).

The Levins model we used above assumes not only an infinite number of habitat patches but also the non-infection of colonization by distance. Since movements of most organisms are restricted in space and hence all patches in a large network are not likely to be equally accessible from a given patch, these assumptions seem contradictory (Hanski, 1999). However, what is really underlying these assumptions is that the model assumes all patches are equally connected to other patches, which is called the mean-field assumption. Although this assumption is at the heart of many ecological theories, it ignores much of what is important about the dynamics of ecological interactions. Ecological interactions such as predation, resource competition, parasitism, epidemic transmission, and reproduction often occur at spatial scales much smaller than that of the whole population (Dieckmann et al., 2000). The dispersal and colonization of migrants in metapopulations are certainly local processes in space, and hence the distribution cannot be described by the mean-field approximation.

The most powerful approach to modeling spatially structured population dynamics and local processes in ecology is the lattice or cellular automation models, which have been widely applied to the researches of metapopulation dynamics and more general questions of

spatial ecology (Tilman and Kareiva, 1997). These spatially explicit simulation models can be analyzed by a useful approach, called the pair approximation and introduced by Matsuda et al. (1992) to ecological research. This approximation, firstly from statistical physics (Katori and Konno, 1991; Tainaka, 1993), has been carried out for many models of population dynamics of plants (Iwasa et al., 1991; Harada and Iwasa, 1994; Harada et al., 1995).

In the framework of metapopulations and spatially structured populations (Sato and Iwasa, 2000; Hui and Li, 2004), two variables are important to describe the distribution of species: global density p_+ and local density $q_{+/+}$. The global density is the probability that a randomly chosen sample is occupied by a local population, indicating the occupancy in a binary (presence/absence) map (Hanski, 1999; McGeoch and Gaston, 2002; Hui and Li, 2003). Local density describes the spatial correlation and indicates the conditional probability that a randomly chosen adjacent quadrate sample of a presence quadrate is also occupied (Dieckmann et al., 2000; Sato and Iwasa, 2000; Hui and Li 2004). As mentioned above about the joint-count statistics, the definition of distribution patterns in a spatial sense can be obtained by the comparison between occupancy p_+ and spatial correlation $q_{+/+}$ (Hui et al., 2006; Hui and McGeoch, 2007b).

According to the processes of metapopulations and Matsuda's model (Matsuda et al., 1992; also in Sato and Iwasa, 2000), the metapopulation dynamics can be described by pair approximation as follows,

$$\begin{aligned}\frac{dp_+}{dt} &= wq_{+/0}(1-p_+) - mp_+ \\ \frac{dp_{++}}{dt} &= 2wp_{+0}\left(\frac{1}{z} + \frac{z-1}{z}q_{+/0+}\right) - 2mp_{++}\end{aligned} \tag{9}$$

where + (occupied by a local population) and 0 (empty) are the state of a patch, p_{+0} ($p_{+0} = p_+ - p_{++}$) and p_{++} are the probabilities that a randomly chosen pair of nearest-neighbor patches are in state +0 and ++, respectively, $q_{+/0}$ ($q_{+/0} = p_{+0}/(1-p_+)$) is the conditional probability that a randomly chosen neighbor of a patch in state 0 is in state +, z is the number of neighbor patches and means the dispersal region of migrants. Equation (9) is analogous to equation (4). For a given empty patch, every local population in the habitat can contribute to the colonization of this patch by the mean-field approximation (the term wp_+), while only local populations in the neighboring patches can colonize the patch by pair approximation (the term $wq_{+/0}$). As for the dynamics of p_{++}, a chosen pair patches in state ++ may come from by colonization (or lead to by extinction) pair patches in state +0 or 0+ (since $p_{+0} = p_{0+}$, there is a term '2' in the equation). The empty patch in the pair +0 can be colonized by the local population in this pair (the term $2wp_{+0}/z$) or the local populations in the neighboring patches of this pair (the term $2wp_{+0}q_{+/0+}(z-1)/z$). Therefore, the colonization of an empty patch and the colonization of a pair +0 (or 0+) are determined by the term $q_{+/0}$ and the term $(1+(z-1)q_{+/0})/z$ (noted that $q_{+/0+} = q_{+/0}$ in pair

approximation) (Hui and Li, 2004). Equation (9) can give the dynamics of the global (or singlet) densities p_+ and the doublet densities p_{++}, through which we can calculate the local densities $q_{+/+}$. According to the formula of conditional probabilities, we also have the formula $p_+(dq_{+/+}/dt) = (dp_{++}/dt) - q_{+/+}(dp_+/dt)$ and $q_{+/+} = p_{++}/p_+$ to transform the dynamics (9) into those of global and local densities (Hui and Li, 2004).

The stability of equilibriums and the trajectories of equation (9) can be easily obtained, as there is only one nontrivial attractive point (stable node) in the phase plane of p_+ and $q_{+/+}$ (the available region is across $0 \le p_+, q_{+/+} \le 1$) as follows,

$$\hat{p}_+ = 1 - \frac{(z-1)m}{(z-1)w - m} \text{ and } \hat{q}_{+/+} = 1 - \frac{m}{w}. \tag{10}$$

Let Θ be the dispersal area (for continuous dispersal curve, $\Theta = \pi \cdot r^2$, where r is the kernel distance of dispersal) and a the grain size of sample of cell, we have $z = \Theta / a$ and,

$$p_+ = \frac{\Theta q_{+/+} - a}{\Theta + q_{+/+}a - 2a} \tag{11}$$

This could be an inner connection between global density and local density that the joint-count statistics can not reveal.

SPATIAL SCALING PATTERNS

As mentioned above, two issues are involved in the analysis of species distribution, spatial and scaling. Using the joint count statistics, we can scale up the sample size (grain) using a Bayesian approximation (Hui et al., 2006). As shown in Figure 3, the absence probability $p_0(a)$ and the correlation of two adjacent empty patches $q_{0/0}(a)$ as scaling up (grain from a to $4a$) will be,

$$\begin{aligned} p_0(4a) &= p_0(a) \cdot q_{0/0}(a)^2 \cdot b_0(a) \\ q_{0/0}(4a) &= q_{0/0}(a) \cdot b_0(a)^2 \end{aligned} \tag{12}$$

where $b_0(a)$ is the probability that a sample patch with two empty neighboring patches is absent. If we choose a Bayesian estimation for $b_0(a)$ (Pitman, 1993), it will be,

$$b_0(a) = \frac{q_{0/0}(a)^2 p_0(a)}{q_{0/0}(a)^2 p_0(a) + q_{0/+}(a)^2 p_+(a)} \tag{13}$$

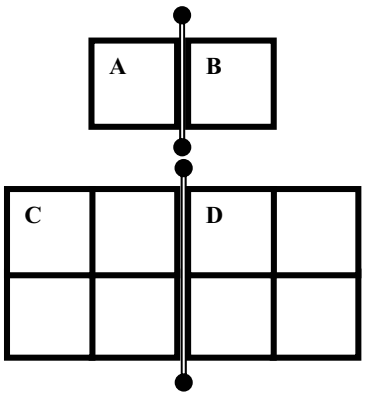


Figure 3. A grain unit (A) and its neighboring unit (B); a chessboard with four times larger grain (C) and its neighbor (D). The lines with knobs indicate the boundary between two samples.

According to probability rules that $p_+ = 1 - p_0$ and $q_{+/+} = 1 - (1 - q_{0/0}) \cdot p_0 / p_+$, Hui, McGeoch and Warren (2006) presented a formula governing the pattern of the occupancy and spatial correlation when scaling up (Figure 4).

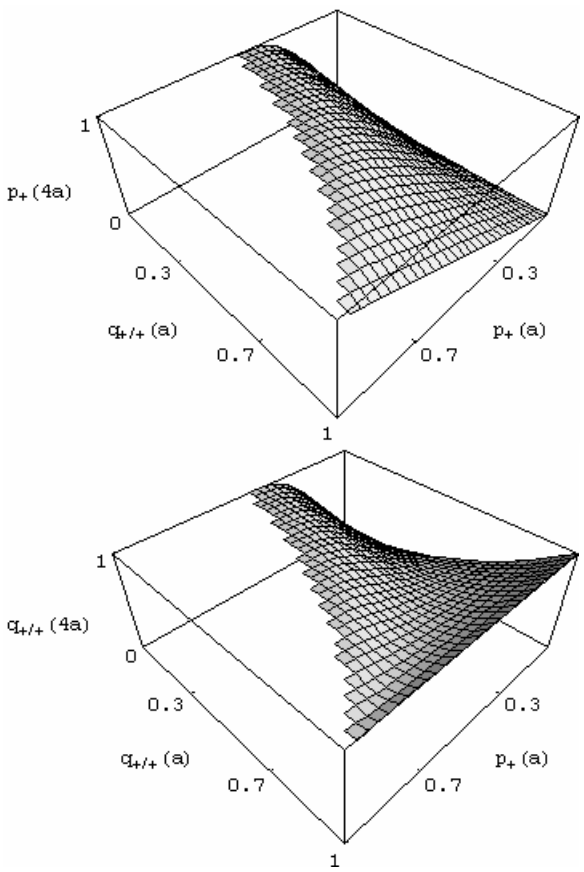


Figure 4. The occupancy and spatial correlation as scaling up. The surface plot only shows in the feasible region of probabilities $0 \le p_+(a) \le 1$ and $2 - 1/p_+(a) \le q_{+/+}(a) \le 1$ (Hui et al., 2006).

An important result here is that the occupancy $p_+(a)$ and spatial correlation $q_{+/+}(a)$ will both limit to 1 with the increase of grain (Figure 4), which means that the spatial distribution of species will change from aggregation to randomness with scaling-up ($p_+(a) = q_{+/+}(a)$). Additionally, segregation will also limit to randomness with scaling-up. Spatial randomness is insensitive to spatial scales. It implies that spatial heterogeneity will decrease with spatial scale and the spatial distribution will tend to randomness with scaling-up. Data from *Azorella selago* also supported this result (Le Roux and McGeoch, 2004) as shown in Figure 5. Based on the above model, we can have a quick test of the spatial distribution pattern, by comparing the occupancy in a chessboard (described by equation (3), as in Figure 3C, D) with the one in a transect (four unit in a line, which has longer boundary than the chessboard sample with similar area; $p_0(4a) = p_0(a) \cdot q_{0/0}(a)^3$), we found that the occupancy will be larger in longer-edge sample if spatial distribution is aggregation but will be smaller if it is segregation in samples with similar sample area or grain (Hui et al., 2006).

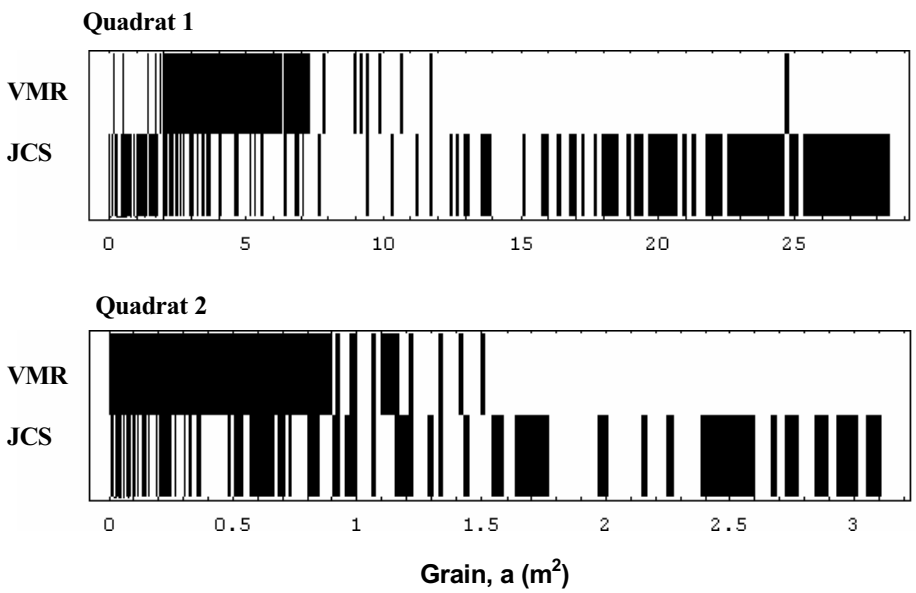


Figure 5. Distribution patterns of cushion plant *Azorella selago* on Marion Island (46°55`S, 37°45`E) from the statistical (the variance-mean ratio, VMR) and the spatial perspectives (the joint-count statistics, JCS). Two plot are based on coordinates of 400 individuals in two quadrats, with each one 200 (Le Roux and McGeoch, 2004). Two bars in each plot indicate the distribution patterns in statistical sense (above; white: aggregation; black: randomness or uniform) and in spatial sense (below; white: aggregation; black: randomness or segregation). Grain is $\pi \cdot r^2$ m^2, where r from 0.01 to 3m with interval of 0.01m for the top plot and from 0.001 to 1m with interval of 0.005m for the bottom plot. For each grain, circle sample and ellipse sample (the ratio of major to minor radiuses is 5) are separated adopted for 500 times independent samples, from which obtain the mean abundance, variance, and occurrence.

This prediction can explain the puzzle of why the density for most intertidal macrofauna has a lower density but has a higher density estimation of *Bathyporeia guilliamsoniana* in rectangular samples, compared to the density observed in square samples with similar area (De Grave and Casey, 2000). The reason might be that most species are aggregated in space while *B. guilliamsoniana* distributes in a segregated fashion due to its high mobility.

Now we present a scaling metapopulation model to explain the biological reason leading to this tendency in spatial patterns of species distribution. If we only consider local dispersal and demographic stochasticity but neglect other ecological factors, such as the Allee effect, genetic structure and habitat destruction (Hanski, 1999; Hui and Li, 2003; Hui and Yue, 2005), the metapopulation dynamical model of the global and local densities by pair approximation will be like equation (9) (Matsuda et al., 1992; Sato and Iwasa, 2000; Hui and Li, 2004), except parameters become scale-sensitive. Let m_a and w_a be the extinction rate (or mortality) and colonization rate on the patch of grain a; z_a is the number of neighbor patches ($z_a a$ means the dispersal region of migrants). Variables $p_{+0}(a)$ and $p_{++}(a)$ are the probabilities that a randomly chosen pair of nearest neighbor patches are in state +0 (one occupied; the other empty) and ++ (both are occupied), respectively. $q_{+/0}(a)$ is the conditional probability that a randomly chosen neighbor of a empty patch is occupied.

Because migrants colonize the empty patch through the boundary, the colonization rate should be proportional to the perimeter of sample, $w_a = w_0 a^{1/2}$, where w_0 is the colonization rate per unit area. According to the extinction model of Hanski (1999), the extinction rate can be described by, $m_a = m_0 a^{-s}$, where m_0 is the extinction rate per unit area and s is a positive constant (in most situation, $0 < s < 1$). Because the dispersal region will not be affected by the sampling area or grain, the number of neighboring patches should be $z_a = z_0 / a$, where z_0 is the number of neighboring patches per unit area. Substituting these three relationships into equation (10), we can obtain the following scaling relationship,

$$\hat{p}_+(a) = 1 - \frac{(z_0 a^{-1} - 1) m_0 a^{-s}}{(z_0 a^{-1} - 1) w_0 a^{1/2} - m_0 a^{-s}}$$

$$\hat{q}_{+/+}(a) = 1 - \frac{m_0}{w_0} a^{-(s+1/2)} \tag{14}$$

It implies that the metapopulation equilibrium of global and local densities will both limit to one with spatial scale (grain a) and consists of the result of spatial patterns above from the statical approach.

The connections between equations (12), (13) and (14) become very complicated. However random distribution is a bridge for us to cross the boundaries and explore the possibility of connections between spatially implicit and explicit perspectives and between experimental statistics and spatial modelling. If the exponent b equals to one in Taylor's power law, it depicts the statistical randomness and can be described by Poisson process. By Poisson process, the probability of finding at least one individual in samples (i.e. occurrence

or occupancy), as mentioned above, will be $p_+(a) = 1 - Exp(-a \cdot d)$ except the scale-sensitivity here. According to the definition of spatial randomness ($p_+(a) = q_{+/+}(a)$), from equations (12) and (13), we have $1 - p_+(4a) = (1 - p_+(a))^4$ and $q_{+/+}(4a) = p_+(4a)$. The first term implies $p_0(x \cdot y) = p_0(y)^x$. Mathematically speaking, the only function that coincides with this condition is the exponential function $p_0(a) = Exp(-a \cdot d)$, which means $p_+(a) = q_{+/+}(a) = 1 - Exp[-a \cdot d]$. This inosculation indicates, on the one hand, the correctness of model for describing spatial patterns, and on the other hand, the similarity between the spatially implicit (Poisson process) and explicit definitions of random distributions.

Moreover, under the mean-field assumption that all patches are equally connected to other patches (Hanski, 1999), the metapopulation dynamics (4) will show randomness in spatial habitat (Sato and Iwasa, 2000; Hui and Li, 2004), which means the global density will converge to the local density in equation (14) as the neighboring number z_0 increases, $p_+(a) \to q_{+/+}(a)$. Two results can be obtained here. First, the global and local densities will both converge to one with scaling-up. Second, there is still some difference. The mechanistic approach leads to a power relationship between absence probability $1 - p_+(a)$ and grain a, but the Poisson process leads to an exponential relationship. This might arise from the classical assumption in metapopulations and spatially structured populations. In the extinction model of Lande (1993), Foley (1994) and Middleton et al. (1995), the asymptotic extinction risk is $m_a \sim K^{-s}$, from which Hanski (1994) obtained the extinction rate $m_a = m_0 a^{-s}$, under the assumption of a power relationship between patch area and the population ceiling, $K \sim a^{\xi}$, where ξ is a constant (Moilanen et al., 1998). The shortcoming of power relationships is that the global and local densities will become negative with the decreasing of grain. It means that you cannot find species (occupancy is zero or negative) if the sample size is too small (i.e. the lattice gridlines are too fine). If we suppose an exponential form of extinction and colonization rate as, $m_a / w_a = Exp[-a \cdot d]$, the global and local densities in equations (14) will be,

$$\begin{aligned} \hat{p}_+(a) &= 1 - \frac{(z_0 / a - 1) Exp[-a \cdot d]}{(z_0 / a - 1) - Exp[-a \cdot d]} \\ \hat{q}_{+/+}(a) &= 1 - Exp[-a \cdot d] \end{aligned} \tag{15}$$

from which, we can obtain an estimation from an occupancy-abundance relationship,

$$u_a = -\ln\left(\frac{1 - p_+(a)}{z_a - p_+(a)}\right) \tag{16}$$

It implies that the random distribution is a bridge not only between the spatial and statistical senses of species distributions but also between the empirical and theoretical approaches, from which we can build an abundance-range size relationship (the same as the occupancy-abundance relationship) not only in the statistical sense (Kunin, 1998; He and Gaston, 2000, 2003), but also in the spatial sense, i.e. a scaling relationship of occupancy, spatial correlation and abundance (Hui et al., 2006; Hui and McGeoch, 2007c). Further work might lie on both sides: 1) experimental tests about the occupancy-abundance relationship and compare with other estimating formulae of abundance from occupancy (Kunin, 1998; He and Gaston, 2000, 2003); 2) we have combined the joint-count statistics and the pair approximation (mechanistic) here, from which a abundance occupancy relationship is obtained. However, the joint-count statistics is a very simple spatial autocorrelation indicator, so is the pair approximation in mathematics. If we combine more advanced or accurate methods (that includes more spatial and statistical information), a group of powerful relationships between life history traits and distribution patterns, and between for example occupancy and abundance could be found. This connection could be a new integrated platform for macroecological and spatial ecological studies.

FUTURE DIRECTIONS

Species distribution are a reflection of species life-history trade-offs, environmental gradients and demographic dynamics (Bolker and Pacala, 1999; Hanski, 1999; Holt and Keitt, 1999; Gaston, 2000; Hui and Li, 2004; Hui, 2007b). It is important to distinguish these spatial patterns from different perspectives. Different concepts will lead to different results on spatial patterns and heterogeneity (Li and Reynolds, 1995; Veldtman and McGeoch, 2004). However, this separation could lead to confusion when scientific synthesis is needed. For example, with scaling-up, species distributions will always change from randomness to aggregation in the statistical sense, but change from aggregation to randomness in the spatial sense. Ten merging problems in spatial ecology and macroecology that could be solved using this communication between experimental statisticians and mathematical ecologists are:

- A synthesis and simplified indicator of species aggregation.
- An occupancy-abundance relationship taking aggregation and spatial scales into account.
- Mechanisms behind Taylor's power law.
- Understanding the interconnection between the dynamic trends of abundance and species range size.
- Predicting the distribution dynamics and pattern of species by its life-history traits.
- Measuring species' life-history traits by their spatial distribution patterns.
- The relationship between co-occurrence of species (nestedness) and the relative abundance curve.
- The relationship between occupancy frequency distributions and abundance frequency distributions in a community.
- The frequency distribution of aggregation in a community.
- The scaling sensitivity of biodiversity structure.

These ten problems have the same characters as they also heavily involve the participation from both sides, experimentally and theoretically. All these problems have already been explored for a while from either side yet with little communication in between. The clear solution of these problems will help us ultimately understand how a species distributes its individuals in space and what it looks like at different resolutions, as well as the relationships among them. An ecological community is a half-neutral system. To some extent, neutral theory can fit the observed patterns quite well (e.g. Hubbell, 2001). However, non-neutral theory, such as niche modeling, can also provide relatively reliable patterns in communities (e.g. Tilman, 2004). These pattern formations from individuals to community scales are elegantly balanced by the forces of natural selection and self-organization. While natural selection plays an important role in choosing who the actor is, the pattern formation in a community or an ecosystem is generally self-organized by those actors, which performs the spatiotemporal patterns and functions at a higher level (community and ecosystem function and service). Understanding these complexity processes of pattern formation requires collaboration within different fields of ecology as well as interdisciplinary communication. Here, breaking the boundaries of spatial analysis and modelling will be a test stone to knock the door of the future.

ACKNOWLEGEMENTS

I would like to thank M.A. McGeoch, Z. Li, M. Warren, X.Z. Han, F. Zhang and R. Veldtman for discussions, P.C. Le Roux for the data of *Azorella selago*, S.H. Hurlbert for his interesting reprints on "Unicorn", B. Laniewski for her editorial help, F. Columbus for the invitation, and DST-NRF Centre for Invasion Biology for funds.

REFERENCES

Allee, W. C. (1931). *Animal aggregations: a study in general sociology*. Chicago: University of Chicago Press.

Allee, W. C. (1938). *The social life of animals*. New York: Norton.

Anderson, R. M. and May, R. M. (1988). Epidemiological parameters of HIV transmission. *Nature, 333*, 514-519.

Anselin, L. (1995). Local indicators of spatial association – LISA. *Geographical Analysis, 27*, 93-116.

Asmussen, M. A. (1979). Density-dependent selection. 2. The Allee effect. *American Naturalist, 114*, 796–809.

Axelrod, R. and Hamilton, W. D. (1981). The evolution of cooperation. *Science, 211*, 1390-1396.

Axelrod, R. M. (1984). *The evolution of cooperation*. New York: Basic Books.

Begon, M., Harper, J. L., and Townsend, C. R. (1996). *Ecology: Individuals, Populations and Communities* (3rd edition). Oxford: Blackwell.

Bolker, B. M. and Pacala, S. (1999). Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *American Naturalist, 153*, 575-602.

Clark, L. R., Geier, P. W., and Hughes, R. D. (1967). *The ecology of insect populations in theory and practice*. London: Methuen.

Czaran, T. and Bartha, S. (1992). Spatiotemporal dynamics models of plant populations and communities. *Trends in Ecology and Evolution, 7*, 38–42.

De Grave, S. and Casey, D. (2000) Influence of sampler shape and orientation on density estimates on intertidal macrofauna. *Journal of the Marine Biology Association of the United Kingdom, 80*, 1125-1126.

Dieckmann, U., Law, R., and Metz, A. J. A. (2000). *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge: Cambridge University Press.

Dobzhansky, T. (1970). *Genetics of the evolutionary process*. New York: Columbia University Press.

Downing, J. A. (1986). Spatial heterogeneity: evolved behaviour or mathematical artifact? *Nature, 323*, 255-257.

Dungan, J. L., Perry, J. N., Dale, M. R. T., Legendre, P., Citron-Pousty, S., Fortin, M.-J., Jakomulska, A., Miriti, M. and Rosenberg, M. S. (2002). A balanced view of scale in spatial statistical analysis. *Ecography, 25*, 626-640.

Durrett, R. and Levin, S. (1994). Stochastic spatial models: a user's guide to ecological applications. *Philosophic Transactions of the Royal Society, London, Series B, 343*, 329–350.

Elliott, J. M. (1977). *Some methods for the statistical analysis of samples of benthic invertebrates* (Second Edition). Cumbria: The Freshwater Biological Association.

Fielding, A. H. and Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation, 24*, 38-49.

Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford: Clarendon.

Foley, P. (1994). Predicting extinction times from environmental stochasticity and carrying capacity. *Conservation Biology, 8*, 124-137.

Ford, E. B. (1940). Genetic research in the Lepidoptera. *Annals of Eugenics, 10*, 227–252.

Fortin, M.-J., Dale, M. R. T., and ver Hoef, J. (2002). Spatial analysis in ecology. In A. H. El-Shaarawi and W. W. Piegorsch (Eds.), *Encyclopedia of environmetrics* (pp. 2051-2058). New York: Wiley and Sons.

Gaston, K. J. and Blackburn, T. M. (2000). *Pattern and process in macroecology*. Oxford: Blackwell.

Gaston, K. J. (2000). Global patterns in biodiversity. *Nature, 405*, 220-227.

Gause, G. F. (1935). *The struggle for existence*. Baltimore: Williams and Wilkins.

Gisiger, T. (2001). Scale invariance in biology: coincidence or footprint of a universal mechanism? *Biological Reviews, 76*, 161-209.

Haldane, J. B. S. (1930). A note on Fisher's theory the origin of dominance and linkage. *American Naturalist, 64*, 87–90.

Hamilton, W. D. (1964). The genetical evolution of social behaviour I. *Journal of Theoretical Biology, 7*, 1-16.

Han, X., Li, Z., Hui, C., and Zhang, F. (2006). Polymorphism maintenance in a spatially structured population: a two-locus genetic model of niche construction. *Ecological Modelling, 192*, 160-174.

Hanski, I. and Gilpin, M. E. (1997). *Metapopulation biology: ecology, genetics and evolution*. New York: Academy Press.

Hanski, I. and Zhang, D. Y. (1993). Migration, metapopulation dynamics and fugitive co-existence. *Journal of Theoretical Biology, 163*, 491-504.

Hanski, I. (1991a). Reply to Nee, Gregory and May. *Oikos, 62*, 88–89.

Hanski, I. (1991b). Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of Linnaean Society, 42*, 17–38.

Hanski, I. (1994). A practical model of metapopulation dynamics. *Journal of Animal Ecology, 63*, 151-162.

Hanski, I. (1998). Metapopulation dynamics. *Nature, 396*, 41-49.

Hanski, I. (1999). *Metapopulation Ecology*. New York: Oxford University Press.

Harada, Y. and Iwasa, Y. (1994). Lattice population dynamics for plants with dispersing seeds and vegetative propagation. *Researches on Population Ecology, 36*, 237–249.

Harada, Y., Ezoe, H., Iwasa, Y., Matsuda, H., and Sato, K. (1994). Population persistence and spatially limited social interaction. *Theoretical Population Biology, 48*, 65–91.

Harms, W. (1999). Biological altruism in hostile environments. *Complexity, 5*, 23–28.

Harrison, J. A., Allan, D. G., Underhill, L. G., Herremans, M., Tree, A. J., Parker, V., and Brown, C. J. (1997). *The atlas of southern Africa*. Johannesburg: BirdLife South Africa.

Hartley, S. and Kunin, W. E. (2003). Scale dependency of rarity, extinction risk, and conservation priority. *Conservation Biology, 17*, 1559-1570.

Hassell, M. P., Comins, H. N., and May, R. M. (1991). Spatial structure and chaos in insect populations. *Nature, 353*, 255-258.

Hassell, M. P., Comins, H. N., and May, R. M. (1994). Species coexistence and self-organizing spatial dynamics. *Nature, 370*, 290-292.

Hastings, A. (1994). Conservation and spatial structure: theoretical approaches. In S. A. Levin (Ed.), *Frontiers in Mathematical Biology* (pp. 494–503). New York: Springer.

He, F. and Gaston, K. J. (2000). Estimating species abundance from occurrence. *American Naturalist, 156*, 553-559.

He, F. and Gaston, K. J. (2003). Occupancy, spatial variance, and the abundance of species. *American Naturalist, 162*, 366-375.

He, F. and Legendre, P. (2002). Species diversity patterns derived from species-area models. *Ecology, 83*, 1185-1198.

Hoffmann, R. (2000). Twenty Years On: The Evolution of Cooperation Revisited. *Journal of Artificial Social and Society Simulation, 3*, http://www.soc.surrey.ac.uk/JASSS/3/2/forum/1.html.

Holt, A. R., Gaston, K. J. and He, F. (2002). Occupancy-abundance relationships and spatial distribution: a review. *Basic Applications in Ecology, 3*, 1-13.

Holt, R. D. and Keitt, T. H. (1999). Alternative causes for range limits: a metapopulation perspective. *Ecology Letters, 3*, 41-47.

Horn, H. S. and MacArthur, R. H. (1972). Competition among fugitive species in a harlequin environment. *Ecology, 53*, 749-752.

Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton: Princeton University Press.

Huffaker, C. B. (1958). Experimental studies on predation: dispersion factors an predator-prey oscillations. *Hilgardia, 27*, 343-383.

Hui, C. (2004). Spatial chaos of metapopulation incurred by Allee effect, overcrowding effect and predation effect. *Acta Botanica Boreali-Occidentalia Sinica, 24*, 370-383.

Hui, C. (2006). Carrying capacity, population equilibrium, and environment's maximal load. *Ecological Modelling, 192*, 317-320.

Hui, C. (2007a). Negative correlation between dynamical complexity and metapopulation persistence: a reply. *Ecological Modelling, 200*, 271-272.

Hui, C. (2007b). On species-area and species accumulation curves: a comment on Chong and Stohlgren's index. *Ecological Indicators*, in press.

Hui, C. and Li, Z. (2003). Dynamical complexity and metapopulation persistence. *Ecological Modelling, 164*, 201-209.

Hui, C. and Li, Z. (2004). Distribution patterns of metapopulation determined by Allee effects. *Population Ecology, 46*, 55-63.

Hui, C. and McGeoch, M. A. (2006). Evolution of body size, range size, and food composition in a predator-prey metapopulation. *Ecological Complexity, 3*, 148-159.

Hui, C. and McGeoch, M. A. (2007a). A self-similarity model for the occupancy frequency distribution. *Theoretical Population Biology, 71*, 61-70.

Hui, C. and McGeoch, M. A. (2007b). Spatial patterns of prisoner's dillema game in metapopulations. *Bulletin of Mathematical Biology, 69*, 659-676.

Hui, C. and McGeoch, M. A. (2007c). Capturing the "droopy-tail" in the occupancy-abundance relationship. *Écoscience, 14*, 103-108.

Hui, C. and Yue, D. X. (2005). Niche construction and polymorphism maintenance in metapopulations. *Ecological Research, 20*, 115-119.

Hui, C., Li, Z., and Yue, D. (2004). Metapopulation dynamics and distribution, and environmental heterogeneity induced by niche construction. *Ecological Modelling, 177*, 107-118.

Hui, C., McGeoch, M. A., and Warren, M. (2006). A spatially explicit approach to estimating species occupancy and spatial correlation. *Journal of Animal Ecology, 75*, 140-147.

Hui, C., Zhang, F., Han, X., and Li, Z. (2005). Cooperation evolution and self-regulation dynamics in metapopulation: stage-equilibrium hypothesis. *Ecological Modelling, 184*, 397-412.

Hurlbert, S. H. (1990). Spatial distribution of the montane unicorn. *Oikos, 58*, 257-271.

Hutchinson, G. E. (1961). The paradox of the plankton. *American Naturalist, 95*, 137-147.

Iwasa, Y., Sato, K., and Nakashima, S. (1991). Dynamic modeling of wave regeneration (Shimagare) in subalpine Abies forests. *Journal of Theoretical Biology, 152*, 143-158.

Kadmon, R., Farber, O., and Danin, A. (2003). A systematic analysis of factors affecting the performance of climatic envelope models. *Ecological Applications, 13*, 853-867.

Katori, M. and Konno, N. (1991). Upper bounds for survival probability of the contact process. *Journal of Statistical Physics, 63*, 115–130.

Keeling, M. and Grenfell, B. (1999). Stochastic dynamics and a power law for measles variables. *Philosophic Transactions of the Royal Society, London, Series B, 354*, 769-776.

Keitt, T. H., Lewis, M. A., and Holt, R. D. (2001). Allee effects, invasion pinning, and species' borders. *American Naturalist, 157*, 203–216.

Kendal, W. S. (2004). Taylor's ecological power law as a consequence of scale invariant exponential models. *Ecological Complexity, 1*, 193-209.

Kimura, M. (1983). *The neutral theory of molecular evolution*. Cambridge: Cambridge University Press.

Kojima, K. and Yarbrough, K. M. (1967) Frequency-dependent selection at the esterase 6 locus in a population of Drosophila melanogaster. *Proceedings of National Academy of Science USA, 57*, 645–649.

Kunin, W. E. (1998). Extrapolating species abundance across spatial scales. *Science, 281*, 1513-1515.

Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist, 142*, 911-927.

Le Roux, P. C. and McGeoch, M. A. (2004). The use of size as an estimator of age in the sub-Antarctic cushion plant, Azorella selago (Apiaceae). *Arctic, Antarctic, and Alpine Research, 36*, 608-616.

Lehman, C. L. and Tilman, D. (1997). Competition in spatial habitats. In D. Tilman and P. Kareiva (Eds.), *Spatial ecology: the role of space in population dynamics and interspecific interactions* (pp. 185-203). Princeton: Princeton University Press.

Levin, S. A. and Paine, R. T. (1974). Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences USA, 71*, 2744-2747.

Levin, S. A. (1974). Dispersion and population interactions. *American Naturalist, 108*, 207–228.

Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology, 73*, 1943-1967.

Levins, R. (1968). *Evolution in changing environments*. Princeton: Princeton University Press.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomology Society of America, 15*, 237–240.

Li, H. and Reynolds, J. F. (1995). On definition and quantification of heterogeneity. *Oikos, 73*, 280-284.

Liebhold, A. M., Rossi, R. E., and Kemp, W. P. (1993). Geo-statistics and geographic information systems in applied insect ecology. *Annual Reviews of Entomology, 38*, 303-327.

Lloyd, M. (1967). Mean crowding. *Journal of Animal Ecology, 36*, 1-30.

Matsuda, H., Ogita, A., Sasaki, A., and Sato, K. (1992). Statistical mechanics of population: the lattice Lotka-Volterra model. *Progress in Theoretical Physics, 88*, 1035-1045.

May, R. M. (1974). Biological populations with non-overlapping generations: stable points, stable cycles and chaos. *Science, 186*, 645-647.

May, R. M. (1994). The effects of spatial scale on ecological questions and answers. In P. J. Edwards, R. M. May, and N. R. Webb (Eds.), *Large-scale Ecology and Conservation Biology* (pp. 1-17). Oxford: Blackwell.

Maynard Smith, J. (1974). *Models in Ecology*. Cambridge: Cambridge University Press.

McCarthy, M. A. (1997). The Allee effect, finding mates and theoretical models. *Ecological Modelling, 103*, 99–102.

McGeoch, M. A. and Gaston, K. J. (2002). Occupancy frequency distribuitons: patterns, artefacts and mechanisms. *Biology Reviews, 77*, 311-331.

Metz, J. A. J., Mollison, D., and van den Bosch, F. (2000). The dynamics of invasion waves. In U. Dieckmann, R. Law, and J. A. J. Metz (Eds.), *The geometry of ecological*

interactions: simplifying spatial complexity (pp 482–512). Cambridge: Cambridge University Press.

Middleton, D. A., Veitch, A. R., and Nisbet, R. M. (1995). The effect of an upper limit to population size on persistence time. *Theoretical Population Biology, 48*, 277-305.

Miner, B. G., Sultan, S. E., Morgan, S. G., Padilla, D. K., and Relyea, R. A. (2005). Ecological consequences of phenotypic plasticity. *Trends in Ecology and Evolution, 20*, 685-692.

Moilanen, A., Smith, A. T., and Hanski, I. (1998). Long-term dynamics in a metapopulation of the American pika. *American Naturalist, 152*, 530-542.

Moran, P. A. P. (1950). Notes on continuous stochastic phenomena. *Biometrika, 37*, 17-23.

Murray, J. D. (1989). *Mathematical biology*. London: Springer-Verlag.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature, 403*, 853-858.

Nowak, M. and May, R. M. (1992). Evolutionary games and spatial chaos. *Nature, 359*, 826-829.

Nowak, M. A. and Sigmund, K. (1993). A strategy of win-stay, lose-shift that outperforms tit-for-tat in the prisoner's dilemma game. *Nature, 364*, 56–58.

Nowak, M. A. and Sigmund, K. (2004). Evolutionary dynamics of biological games. *Science, 303*, 793–799.

Nowak, M. A., Bonhoeffer, S., and May, R. M. (1994). Spatial games and the maintenance of cooperation. *Proceedings of National Academy of Science USA, 91*, 4877–4881.

Odling-Smee, F. J., Laland, K. N., and Feldman, M. W. (1996). Niche construction. *American Naturalist, 147*, 641–648

Pacala, S. W. (1986). Neighborhood models of plant population dynamics. 2. Multispecies models of annuals. *Theoretical Population Biology, 29*, 262-292.

Pearson, E. S. and Hartley, H. O. (1966). *Biometrika Tables for Statisticians* (Third Edition). Cambridge: Cambridge University Press.

Perry, J. N., Liebhold, A. M., Rosenberg, M. S., Dungan, J. L., Miriti, M., Jakomulska, A. and Citron-Pousty, S. (2002). Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography, 25*, 578-600.

Pickett, S. and Cadenasso, M. L. (1995). Landscape ecology: spatial heterogeneity in ecological systems. *Science, 269*, 331-333.

Pielou, E. C. (1969). *An introduction to mathematical ecology*. New York: John Wiley and Sons.

Pitman, J. (1993). *Probability*. New York: Springer.

Platt, W. and Weis, I. (1977). Resource partitioning and competition within a guild of fugitive prairie plants. *American Naturalist, 111*, 479-513.

Rand, D. A. and Wilson, H. B. (1991). Chaotic stochasticity: a ubiquitous source of unpredictability in epidemics. *Proceedings of the Royal Society of London B*, 246, 179-184.

Roughgarden, J. (1997). Production functions from ecological populations: a survey with emphasis on spatially implicit models. In D. Tilman, and P. Kareiva (Eds.), *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions* (pp. 296-317). Princeton: Princeton University Press.

Sato, K. and Iwasa, Y. (2000). Pair approximation for lattice-based ecological models. In U. Dieckmann, R. Law and J. A. J. Metz (Eds.), *The geometry of ecological interactions: simplifying spatial complexity* (pp. 341-359). Cambridge: Cambridge University Press.

Strickberger, M. W. (2000). *Evolution*. Boston: Jones and Bartlett.

Tainaka, K. (1993). Paradoxical effect in a three-candidate voter model. *Physical Letters A, 176*, 303–306

Taylor, L. R. and Woiwod, I. P. (1982). Comparative synoptic dynamics: 1. Relationships between interspecific and intraspecific spatial and temporal variance-mean population parameters. *Journal of Animal Ecology, 51*, 879-906.

Taylor, L. R. (1961). Aggregation, variance and the mean. *Nature, 189*, 732-735.

Taylor, L. R., Woiwod, I. P. and Perry, J. N. (1978). The density-dependence of spatial behaviour and the rarity of randomness. *Journal of Animal Ecology, 47*, 383-406.

Tilman, D. and Kareiva, P. (1997). *Spatial Ecology: the role of space in population dynamics and interspecific interactions* (Monographs in Population Biology). Princeton: Princeton University Press.

Tilman, D. (1977). Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology, 58*, 338-348.

Tilman, D. (1982). *Resource competition and community structure*. Princeton: Princeton University Press.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology, 75*, 2-16.

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences USA, 101*, 10854-10861.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology, 46*, 35-57.

Upton, G. J. G. and Fingleton, B. (1985). *Spatial data analysis by example, vol. 1: point pattern and quantitative data*. New York: Wiley.

Vance, R. (1984). The effect of dispersal on population stability in one species discrete-space population growth models. *American Naturalist, 123*, 230-254.

Veldtman, R. and McGeoch, M. A. (2004). Spatially explicit analyses unveil density dependence. *Proceedings of the Royal Society of London, Series B, 271*, 2439-2444.

Viet, R. R. and Lewis, M. A. (1996). Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. *American Naturalist, 148*, 255–274.

Walters, S. (2001). Landscape pattern and productivity effects on source-sink dynamics of deer populations. *Ecological Modelling, 143*, 17–32.

Wang, G., Liang, X.-G., and Wang, F.-Z. (1999). The competitive dynamics of populations subject to an Allee effect. *Ecological Modelling, 124*, 183–192.

Warren, M., McGeoch, M. A. and Chown, S. L. (2003). Predicting abundance from occupancy: a test for an aggregated insect assemblage. *Journal of Animal Ecology, 72*, 468-477.

Wiens, J. A. (2000). Ecological heterogeneity: ontogeny of concepts and approaches. In M. J. Hutchings, E. A. Jones, and A. J. A. Stewart (Eds.), *The Ecological Consequences of Environmental Heterogeneity* (pp. 9-31). Oxford: Blackwell Science.

Williams, G. C. (1966). *Adaptation and natural selection*. Princeton: Princeton University Press.

Wilson, D. S. and Sober, E. (1994). Re-introducing group selection to human behavioral sciences. *Behaviour and Brain Science, 17*, 585–654

Wilson, R. J., Thomas, C. D., Fox, R., Roy, D. B., and Kunin, W. E. (2004). Spatial patterns in species distributions reveal biodiversity change. *Nature, 432*, 393-396.

Wolfram, S. (1984). Cellular automata as models of complexity. *Nature, 311*, 419-424.

Wright, S. (1930). The genetical theory of natural selection. *Journal of Heredity, 21*, 349–356.

Wu, J., Jones, K. B., Li, H. and Loucks, O. L. (2006). *Scaling and uncertainty analysis in ecology: methods and applications*. New York: Springer.

Zhang, F., Hui, C., Han, X., and Li, Z. (2005a). Evolution of cooperation in patchy habitat under patch decay and isolation. *Ecological Research, 20*, 461–469.

Zhang, F., Li, Z., and Hui, C. (2005b). Spatiotemporal dynamics and distribution patterns of cyclic competition in metapopulation. *Ecological Modelling, 193*, 721-735.